How imperfect can land sparing be before land sharing is more favourable for wild species?

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Abstract

1. Two solutions, at opposite ends of a continuum, have been proposed to limit negative impacts of human agricultural demand on biodiversity. Under land sharing, farmed landscapes are made as beneficial to wild species as possible, usually at the cost of lower yields. Under land sparing, yields are maximized and land not needed for farming is spared for nature. Multiple empirical studies have concluded land-sparing strategies would be the least detrimental to wild species, provided land not needed for agriculture is actually spared for nature. However, the possibility of imperfections in the delivery of land sparing has not been comprehensively considered.

2. Land sparing can be imperfect in two main ways: land not required for food production may not be used for conservation (incomplete area sparing), and habitat spared may be of lower quality than that assessed in surveys (lower habitat quality sparing). Here we use published data relating population density to landscape-level yield for birds and trees in Ghana (167 and 220 species, respectively) and India (174 birds, 40 trees) to assess effects of imperfect land sparing on region-wide population sizes and hence population viabilities.

3. We find that incomplete area and lower habitat quality imperfections both reduce the benefits of a land-sparing strategy. However, sparing still outperforms sharing whenever ≥28% of land that could be spared is devoted to conservation, or the quality of land spared is ≥29% of the value of that surveyed. Thresholds are even lower under alternative assumptions of how population viability relates to population size and for species with small global ranges, and remain low even when both imperfections co-occur.

4. Comparison of these thresholds with empirical data on the likely real-world performance of land sparing suggests that reducing imperfections in its delivery would be highly beneficial. Nevertheless, given plausible relationships between population size and population viability, land sparing outperforms land sharing despite its imperfections.

5. *Policy implications*. Our results confirm that real-world difficulties in implementing land sparing will have significant impacts on biodiversity. They also underscore the need for strategies which explicitly link yield increases to setting land aside for conservation, and for adoption of best practices when spared land requires restoration. However, land-sparing approaches to meeting human agricultural demand remain the least detrimental to biodiversity, even with current imperfections in implementation.

Keywords: Density-yield curve; Habitat restoration; Imperfect land sparing; Land sharing; Land sparing; Wildlife-friendly farming; Agricultural demand; Biodiversity

52 **Introduction**

53 Agriculture currently covers 40% of the world's ice-free land (Foley et al., 2011), and poses
54 the single greatest threat to biodiversity of any sector (IUCN, 2016). Moreover, with an
55 increasingly large and wealthy human population, agricultural demand is rising quickly
56 (Godfray et al., 2010). Indeed, it is expected that as much food will be produced this half-
57 century as since the beginning of agriculture (DEFRA, 2009). More equitable distribution of
58 food, reduction in post-harvest waste, and switching to more plant-based diets would help
59 limit the footprint of agriculture (Godfray et al., 2010). However, food production is still
60 predicted to increase, so managing land-use to minimise the negative impacts on wild nature
61 is crucial (Foley et al., 2011).

62

63 This concern has prompted two contrasting solutions, at the extremes of a continuum. Land
64 sharing describes the adoption of wildlife-friendly practices (see Tscharntke et al., 2012) such
65 as retaining small patches of unfarmed natural or semi-natural vegetation within farms or
66 adopting production methods that reduce negative effects on wild species living on farms.
67 However, such practices usually lower overall yield – production per unit area of the entire
68 farmed landscape (Green et al., 2005) – such that more land needs to be farmed to produce a
69 given amount of food. In contrast, under land sparing, different landscapes have discrete
70 primary objectives – food production or biodiversity conservation – with high yields on
71 farmland permitting the retention or restoration of native vegetation elsewhere (Green et al.,
72 2005), albeit often at a cost to on-farm biodiversity (Phalan et al., 2011).

73

74 Tests of which approach would be better for biodiversity involve quantifying how the
75 population densities of wild species respond to agricultural yield (Green et al., 2005). So-
76 called density-yield curves, describing the relationship between individual species'

77 population density and agricultural yield, are derived from field surveys of large (typically
78 1km^2) sample areas with comparable soils, climate and topography, but different land-uses
79 (including some sample areas supporting native vegetation). For any specified level of
80 region-wide production, fitted density-yield functions are used to estimate each species' total
81 population size, given a particular yield on farmed land and assuming that land not required
82 to meet this level of production supports vegetation similar to that of the non-farmed land
83 surveyed. For a given total production level, species' regional population sizes are predicted
84 for all yields between the lowest permissible (which requires the entire region to be farmed to
85 deliver the specified production level: land sharing) and the highest possible (where all land
86 not needed is assigned to native vegetation: land sparing). It is then possible to tally the
87 numbers of species that would have their highest regional population with farming at the
88 lowest permissible yield, the highest possible yield or at some intermediate yield.
89
90 Studies of birds and trees in Ghana and India (Phalan et al., 2011); birds in Uganda (Hulme et
91 al., 2013); birds in Kazakhstan (Kamp et al., 2015); birds, dung beetles, Asteraceae and
92 grasses in the pampas (Dotta, 2013); and birds, trees and dung beetles in Mexico (Williams et
93 al., 2017) have all reached the same conclusion. Extreme land sparing is associated with
94 larger total population sizes for more species than extreme land sharing or any intermediate-
95 yield approach. This conclusion applies for current production levels; and as total production
96 (as is likely) the advantage of sparing over sharing increases. Hence if it could be delivered in
97 practice, land sparing would be the least bad option for wild nature in all these regions.
98 Indeed we are unaware of any study which quantifies yields, examines both native vegetation
99 and high-yield landscapes, and uses population-based metrics of biodiversity outcomes, in
100 which sharing out-performs sparing.
101

102 However, the scenarios explored in these studies assume that land sparing is perfect, in two
103 different ways. First, they assume that all land not needed for crop production is maintained
104 under or restored to native vegetation. Second, the native vegetation assessed in field surveys
105 is assumed to be representative, in terms of species' population densities, of land that would
106 be protected or restored through land sparing. In the real world neither of these assumptions
107 holds completely (Ewers et al., 2009; Rey Benayas et al., 2009).
108
109 Yield increases in the real world do not always result in proportionate increases in land
110 spared for native vegetation (Tscharntke et al., 2012; see left of Fig. 1a), for several reasons.
111 Increased farm efficiency may reduce costs of production and hence increase farm profits.
112 Reduced commodity prices could also increase demand, leading to a rebound effect
113 sometimes labelled Jevons paradox (Ewers et al., 2009; Villoria et al 2013; Byerlee et al.,
114 2014). Land potentially spared by yield increases of staple crops might be used to produce
115 luxury or cash crops, or for other land uses (Ewers et al. 2009). Government subsidies may
116 incentivise farmers to produce more than would otherwise be the case (Ewers et al., 2009).
117 Last, land speculation in agricultural frontiers could mean that land is occupied and cleared
118 irrespective of demand for farm products (Baumann et al., 2017; le Polain de Waroux et al.,
119 2018). Any of these mechanisms would encourage farming on land that could otherwise have
120 been spared. In the absence of explicit land-sparing policies, such effects have been observed
121 to reduce the area of land spared to little over 5% of its potential level (Ewers et al., 2009).
122
123 In addition, native vegetation on spared land might be of lower average quality for wild
124 species than that of reference areas surveyed during fieldwork (see right of Fig. 1a), again for
125 several reasons. If the land that is spared was previously farmed, sparing would require its
126 restoration, but restored vegetation is often lower quality than existing vegetation (Rey

127 Benayas et al., 2009; Law and Wilson, 2015; Bull et al., 2017); at least in the short term,
128 pioneer species may dominate, with negative consequences for other species (MacDonald et
129 al., 2000). Second, edge effects, which can reduce population densities close to farmland,
130 might be greater near high-yield farming, leading to densities in spared native vegetation
131 being lower than those observed in field surveys (Didham et al., 2015; Lamb et al., 2016a).
132 Finally, spared land may be poorly protected, as suggested for Tanzania, where agricultural
133 intensification might mean demand for woody products is redirected towards forests rather
134 woodlands on farms (Quandt, 2016). Alternatively, land spared for conservation purposes
135 might be of higher value for wild species than non-farmed areas covered by the field surveys,
136 if land sparing enabled the creation (or protection) of larger habitat tracts. However, such an
137 outcome would only underline the case for land sparing and so is not considered further.
138
139 To our knowledge, no study has yet examined how the relative merits of sparing and sharing
140 change under incomplete area sparing. One element of lower habitat quality sparing was
141 explored in Lamb et al.'s (2016a) study of edge effects, and the potential effects of spared
142 land being of lower quality for wild species than pristine habitat were modelled by Law and
143 Wilson (2015). Here we assess for the first time the effects of both types of imperfection,
144 operating in isolation, and co-occurring, using fieldwork-derived, species-specific density-
145 yield functions to calculate region-wide populations and estimate population viabilities for
146 large numbers of species.
147
148 **Materials and methods**
149 *Landscapes and population sizes*
150 We followed the framework of Green et al. (2005) and Phalan et al. (2011) to compare the
151 effects of meeting region-wide food production targets in contrasting ways. Our perfect two-

compartment model of extreme land sparing (shown by regions on the right of Fig. 1b) comprised high-yield agriculture over an area A_{HY} (in year i for region j) just sufficient to meet the production target (PT) when it is farmed at maximum yield (MY):

(Eq. 1) $$A_{HY\,ij} = \frac{PT_{ij}}{MY_{ij}}$$

with the rest of the region $A_{NV\,ij}$ under native vegetation:

(Eq. 2) $$A_{NV\,ij} = TA_j - A_{HY\,ij}$$

where TA is the total area of the region. Our model of extreme land sharing involves the whole region being farmed at ShY_{ij}, the lowest yield sufficient to just meet the production target:

(Eq. 3) $$ShY_{ij} = \frac{PT_{ij}}{TA_j}$$

We then assessed the region-wide population sizes of wild species under our scenarios using density-yield curves. Under land sharing the population size (P_{Sh}) of species (k) is given by:

(Eq. 4) $$P_{Sh\,k} = TA_j \times PD_{ShY_{ij}\,k}$$

where the species' population density (PD) is that under the lowest-yielding agriculture just sufficient to meet the production target (from Equation 3).

Under land sparing region-wide population sizes are calculated incorporating each of the two types of imperfections of land sparing, which we introduce through a perfection score (ψ) which ranges from 0 to 1. Under incomplete area sparing the amount of land set aside for nature, as a proportion of that which theoretically could be, is gradually reduced to zero (Fig. 1b, upper panel), and the reduction in area spared is translated into a reduction in each species' population size $P_{IA\,k}$:

(Eq. 5) $$P_{IA\,k} = PD_{NV\,k} \times A_{NV} \times \psi_A + PD_{HY\,k} \times \left(TA_j - A_{NV} \times \psi\right)$$

calculated as the product of its population density in native vegetation, the area under native vegetation, and the area perfection score (ψ_A), plus the product of its population density under high yield farming and the area perfection-adjusted area under farming.

Imperfection due to lower habitat quality on spared land results in reduced population density in spared land (Fig. 1b, lower panel), which decreases each species' population size to $P_{LHQ\,k}$:

(Eq. 6) $$P_{LHQ\,k} = PD_{NV\,k} \times \psi_{HQ} \times A_{NV} + PD_{HY\,k} \times (TA_j - A_{NV})$$

calculated as the product of its population density in surveyed native vegetation, the habitat quality perfection score (ψ_{HQ}) and the area under native vegetation, plus the product of population density in high-yield agriculture and the area under farming.

We also considered the effects of the co-occurrence (CO) of incomplete area sparing and lower habitat quality sparing. Each species' population size is then given by:

(Eq. 7) $$P_{CO\,k} = PD_{NV\,k} \times A_{NV} \times \psi_A \times \psi_{HQ} + PD_{HY\,k} \times \left(TA_j - A_{NV} \times \psi_A\right)$$

calculated as the product of its population density in native vegetation, the area under native vegetation, the area perfection score, and the habitat quality perfection score; plus the product of its population density under high yield farming and the area perfection-adjusted area under farming.

To put population sizes under each scenario into context we estimated a baseline pre-agricultural (*PA*) population size, assuming that the entire region was under native vegetation:

(Eq. 8) $$P_{PA\,k} = TA_j \times PD_{NV\,k}$$

We then expressed total population sizes under each scenario as a fraction of this pre-agricultural baseline population. Like previous studies that have adopted the sparing-sharing framework (Phalan et al. 2011; Dotta, 2013; Hulme et al. 2013; Gilroy et al. 2014a; Kamp et al. 2015; Williams et al. 2017), we chose a pre-agricultural baseline as our reference because it is the closest approximation we have to the landscape condition in which a region's species have persisted for most of their existence.

Estimating the viability of populations

We next wanted to translate changes in species' relative population sizes under each scenario into changes in their likely viability. Changes in population viability depend not just on the number of individuals added or removed, but also on initial population size (losing 1000 individuals will clearly reduce the viability of a starting population of 1010 far more than that of a population of 10,000, for example). The increasing impact on viability of losing one

individual increases as population size decreases, implying that the relationship between population size and viability is concave.

We therefore follow others (Thomas et al., 2004; Phalan, 2009) in converting changes in suitable habitat area or population size into changes in population viability using a power-law function with an exponent less than one. Adoption of a similar approach in the context of the IUCN Red List criteria (Clements et al., 2011) was criticised (e.g. Akçakaya et al., 2011) for not using a meaningful baseline to define the point at which a population is certain to persist (i.e. for which viability = 1), and above which viability cannot increase with population size. We tackle this here by expressing the population sizes under our agricultural scenarios relative to those under our pre-agricultural baseline. We then translate these into viabilities, averaged across all K species of a taxon in a region:

(Eq. 9) $$V_{LU} = \begin{cases} \sum_{k=1}^{K} \frac{\left(\frac{P_{LU\,k}}{P_{PA\,k}}\right)^{z}}{K} & if\ \frac{P_{LU\,k}}{P_{PA\,k}} \leq 1 \\ 1 & if\ \frac{P_{LU\,k}}{P_{PA\,k}} > 1 \end{cases}$$

where mean species population viability (V) under different land-use scenarios (LU) is calculated by raising each species' population size relative to the pre-agricultural population size to the power z, and taking the mean of this quantity across all species. We use a range of z-values (0.12, 0.15, 0.18, 0.25, 0.5, 1) reflecting uncertainty in the nature of the relationship between population viability and relative population size. Like others, we consider z-values <0.5 more plausible (Phalan, 2009; Thomas et al., 2004), but include higher values for completeness. Note that if a population exceeds baseline then it is assumed to have a viability of 1. This means "winner" species (whose population densities are higher under farming than

247 in baseline vegetation – Phalan et al., 2011) do not have higher viabilities under agriculture
248 than they would without.
249
250 Clearly Equation 9 does not capture all the intricacies of the relationship between population
251 size and viability, but rather describes a broad pattern. For example, it is possible that Allee
252 effects may cause a sigmoidal relationship, with an inflection point for low population sizes
253 (Dennis, 1989). However, populations of most of our species are too large, under most
254 scenarios, for this simplification to substantially alter our findings.
255
256 *Disaggregating results by global range size*
257 Our analysis enabled us to estimate the effects of imperfect sparing on the average population
258 viability of large sets of species, and in particular the threshold level of perfection – which we
259 term the point of indifference – below which mean population viability is greater under land
260 sharing. However, mean values mask underlying variation across species. We therefore also
261 used Equations 4-6 and 8-9 to calculate the population viability of each individual species at
262 the point of indifference. We then examined the distribution of individual species' population
263 viability estimates, separately for small and large global range species (as defined in Phalan et
264 al. 2011), under each of sharing, incomplete area sparing, and lower habitat quality sparing.
265
266 *Study areas*
267 We parameterised our models using the density-yield curves reported by Phalan et al. (2011)
268 for birds and trees in Ghana and India. The functions were fitted to survey data for 1km^2
269 squares (25 across 9117 km^2 in Ghana, 20 across 2039 km^2 in India) chosen to represent the
270 full variation in yields seen within the study regions and to be similar in terms of climate,
271 topography and soils (so that, all else equal, one would expect similar yields and population

densities). The fitted density-yield curves describe each species' expected mean population density across a 1km^2 block generating a given yield. For this purpose, it was not necessary to describe finer-scale variation in species' abundance.

Phalan et al. (2011) also reported maximum observed and projected yields, and production targets for each region for 2007 and 2050. Across this interval maximum yields were projected to increase by 25% (i.e. at 0.5% per year) and production targets by 94.1% and 58.7% for Ghana and India, respectively (based on data from FAO, 2010).

Expected degree of perfection of land sparing

Finally, to put our results in context we considered the likely degree of perfection that might be expected under land sparing – assuming that no explicit effort is made to reduce imperfection. For incomplete area sparing, we sought a benchmark of "passive sparing" (sensu Phalan et al. 2016, and as described by the Borlaug hypothesis - Stevenson et al., 2013), whereby increased yields lower the area farmed by reducing prices (Barbier and Burgess, 1997); this process has been proposed as an explanation of afforestation and continued protection of native vegetation in India (Ravindranath et al., 2011). The only global quantification of passive sparing – defined as the change in area farmed, per capita of human population, with yield change – comes from Ewers et al. (2009). Although their estimates may incorporate the effects of some broad environmental regulations, they give an indication of the magnitude of land sparing that might be expected in the absence of explicit land-sparing policies. Based on data from 124 countries and 23 staple crops over 20 years they estimate: (1) the average observed proportional decrease in land used for growing 23 staple crops relative to the proportional increase in their yields (0.143; hereafter our upper-bound estimate); and (2) the proportional decrease in land used for all crops relative to the

297 proportional increase in the 23-crop yields (0.054; our lower-bound estimate). The former is
298 more relevant in analyses which involve all crops increasing in yield, while the latter captures
299 expansion of agricultural land dedicated to cash crops.
300
301 We use two perfection scores to benchmark the quality of native vegetation under lower
302 habitat quality sparing; both account for time delays in restoration and for species-specific
303 habitat preferences. The first is the median quality of restored habitat relative to reference
304 habitat reported in a major meta-analysis (0.86; Rey Benayas et al., 2009). The second
305 derives from development operations seeking "no net loss" of native vegetation, which use
306 multipliers to evaluate how much land must be restored in order to compensate for a given
307 area of habitat conversion. The largest multiplier regarded as operationally feasible is 10
308 (Gibbons et al., 2016; Bull et al., 2017), and so we use the reciprocal of this (0.1) as a second
309 illustrative perfection score. It is conceivable that the perfection score for habitat quality for
310 some biodiversity outcomes could be even lower (i.e. near to zero).
311
312 **Results**
313 *Imperfection due to incomplete area sparing*
314 For Ghanaian birds at the 2007 production target the solid teal line in Fig. 2a shows mean
315 species population viability under land sparing given different degrees of perfection and
316 assuming z=1. As in all other cases, imperfect sparing reduces mean population viability.
317 Moving leftwards (away from perfect sparing) this line crosses the dashed teal line – which
318 describes the same species' mean population viability under extreme land sharing – at a
319 perfection score of 0.52. To the right of this point of indifference, incomplete area sparing is
320 less bad for species' persistence, and left of it land sharing is less bad. Lines of different
321 colours show results for alternative z-values (which we consider more plausible than z=1);

these require greater imperfection (perfection scores of 0.01-0.28 for z=0.12-0.5) before land sharing outperforms incomplete area sparing. Note that all land-sharing lines conservatively assume that population densities of species recorded in surveys of low-yield farmland apply across the entire region (which might not be the case – see Discussion).

For Indian birds the levels of perfection required for sharing to outperform incomplete area sparing are lower still (perfection scores of 0.01-0.08 for z=0.12-0.5; Fig. 2c). This pattern is even more marked for trees, in both regions (for z=0.12-0.5, perfection required is 0.01-0.05; Fig. 2b, d) probably because tree population densities are more sensitive to conversion to agriculture than are those of birds. Increasing the production target to meet projected demand for 2050 also results in lower degrees of perfection being required for land sparing to be least bad (for z=0.12-0.5, perfection required is 0.01-0.20; Fig. S1 in Supporting Information).

How do these threshold levels of perfection compare with real-world values? Our upper-bound estimate of passive sparing (0.143; right-hand vertical lines of Fig. 2) exceeds that required for incomplete area sparing to outperform land sharing across all plausible z-values (0.12-0.5; only for Ghanaian birds with $z \geq 0.5$ is this not the case). Under the more conservative assumptions of our lower-bound estimate (i.e. with increased supply cash crops) the level of perfection recorded under passive sparing alone (0.054; left-hand vertical lines) is still generally associated with incomplete area sparing outperforming land sharing (exceptions are for birds with $z \geq 0.5$ and Ghanaian birds under 2007 production with $z \geq 0.25$).

Imperfection due to lower habitat quality of spared land

The results of lowering the quality of native vegetation (Fig. 3) broadly echo those of incomplete area sparing. As with area imperfection, lower habitat quality sparing reduces

mean species population viabilities. The points of indifference are slightly further right than for incomplete area sparing (for z=0.12-0.5, lower habitat quality sparing is better provided perfection exceeds 0.01-0.29). As before, crossover points shift left (relative to those for Ghanaian birds at 2007 production levels, Fig. 3a) for trees (Fig. 3b, d), Indian species (Fig. 3c, d), and 2050 production targets (Fig. S2).

Comparing again with benchmark data, all points of indifference lie to the left of our upper-bound estimate (0.86; right-hand vertical lines in Fig. 3). Moreover for more plausible z-values (0.12-0.5) most points of indifference are left of our lower-bound benchmark (0.1; left-hand vertical lines) – the only exceptions are for $z \geq 0.5$, for Ghanaian birds (at 2007 and 2050 production) and Indian birds (at 2007 production). For most combinations of z-values, study regions, taxa and production target, it is only when the quality of spared land is almost zero that land sharing becomes more favourable.

Co-occurrence of incomplete area and lower habitat quality imperfections

Fig. 4 summarises the relative performance of sparing and sharing when both forms of imperfection operate concurrently. Each curve shows, for a given z-value, the combinations of imperfection scores below which sharing performs better than sparing. Hence for any given taxon, region and z-value line, the y-axis value where x=1 (i.e. when habitat quality perfection=1) is the corresponding point of indifference for imperfect area sparing in Fig. 2; likewise for the same line the x-axis value where y=1 is the point of indifference for imperfect habitat quality sparing in Fig. 3. For combinations of perfection values above the lines which link these points, land sparing outperforms sharing; below these lines, sharing outperforms sparing.

Two findings emerge. For most z-values, both taxa, both regions and both production levels (Fig. S3), land sparing outperforms sharing except when at least one perfection score is very low. At our upper-bound benchmarks (grey circles in Fig. 4), land sparing is still favoured over sharing for $z \leq 0.5$. Even when both types of imperfection are operating at our lower-bound benchmarks (black diamonds in Fig. 4), sparing still outperforms sharing for all cases where $z \leq 0.25$, except for Ghanaian birds. The second observation is that the curves are convex. This means a moderate increase in whichever perfection score is lower can compensate for a (sometimes much) greater decrease in the higher perfection score.

Global range size and population viabilities

The population viabilities of individual small- and large-range species of Ghanaian birds at the point of indifference between sharing and imperfect sparing (in terms of cross-species mean viability) are presented in Fig. 5 (for 2007 production). This disaggregation reveals that sharing and imperfect sparing, even though equivalent in averaged effect, have very different impacts on small- and large-range species. Sharing is associated with lower viability of small-range species and greater viability of large-range species than is either form of imperfect sparing (for Ghanaian trees, Indian birds and trees, and 2050 production, see Table S1 and Fig. S4). This result means that from the perspective of species with small global ranges, even lower degrees of perfection are required before imperfect sparing performs as badly as land sharing.

Discussion

We set out to assess how imperfections in land sparing affect its performance relative to land sharing. In the absence of explicit land-sparing policies, rebound effects, land speculation and

expansion of other land uses all mean yield increases spare less land for native vegetation than is theoretically possible (Ewers et al., 2009; Tscharntke et al., 2012; Carrasco et al 2014), while edge effects, inadequate protection, and poor or delayed restoration mean spared land may be of lower quality for wild species from areas of native vegetation assessed during field surveys (Rey Benayas et al., 2009; Law and Wilson, 2015; Lamb et al., 2016a).

Incorporating these imperfections into models does indeed reduce mean species population viability compared with perfect land sparing. For incomplete area sparing, this underscores the need (highlighted by Phalan et al. 2016) for effective policy mechanisms linking yield increases to the protection of unfarmed land for nature. Examples could include subsidy or loan schemes with coupled incentives for yield improvements and habitat conservation (as in Gola Forest, Sierra Leone; Stand For Trees, 2015), land-use zoning (used in the National Afforestation Programme in India; Ministry of Environment and Forest, 2009), and strategic deployment of yield-enhancing infrastructure away from land conversion frontiers (Laurance et al. 2014; Phalan et al. 2016). Likewise, for sparing to provide as much conservation benefit as possible efforts are needed to limit edge effects, protect spared vegetation and deliver timely, high-quality habitat restoration. But even under pessimistic scenarios for each of these imperfections, and allowing for them to co-occur, land sparing was almost always the least bad option for the taxa we examined. Moreover, even lower degrees of perfection would still outperform sharing for narrowly distributed species, which are typically the main focus of conservation concern.

Our conclusions vary somewhat depending upon the relationship between a population's size and its viability. A better understanding of this relationship is clearly a high priority for conservation. Our approach builds on the methods of Clements et al. (2011) and addresses the

primary criticism of Akçakaya et al. (2011) by including a baseline population size. It is possible that Allee effects mean that the true relationship may not be approximated by a simple power law, but instead be sigmoidal (Dennis, 1989). But Allee effects only occur at very small population sizes, typically well below those in this study. We thus consider that, given the range of *z*-values we explored, we have identified the likely bounds of the level of perfection required for land sparing to achieve higher mean population viabilities than land sharing.

A key feature of our model is that it compares biodiversity outcomes of land-use strategies within regions which are homogeneous for climate, soils and topography. This simplification means our model in its current form is inappropriate for predicting biodiversity outcomes in heterogeneous regions (Macchi et al. 2016). But such areas are often important for conservation (e.g. Struebig et al., 2015), and modelling them within a sparing/sharing framework could be addressed by subdividing them into homogeneous, separately modelled subareas. An alternative could be to compare spatially-explicit land-use scenarios that use information linking each species' population density and agricultural yields to those ecological variables that underpin the region's heterogeneity; in principle this could highlight areas where either production or conservation could be prioritised at minimal cost (Grau et al. 2013), but would require data on causal relationships between covariates, yields and species' abundances that are rarely available. One other framework involves building production-possibility frontiers of land-use for particular regions; results so far have supported land sparing (Law et al., 2015, 2017), but further work is needed using data on a broader suite of species.

446 Our pre-agricultural baselines have limitations. While we believe they are the most
447 appropriate reference point for comparing the outcomes of different scenarios, there are
448 uncertainties in estimating pre-agricultural population densities. Remaining areas of native
449 vegetation have changed since the introduction of farming (Gardner et al., 2009) – in
450 particular in the absence of pre- and post-colonial human influences (such as the extirpation
451 of many large mammals), the mixture of successional stages in some landscapes may have
452 been different. Collecting sufficient information to account for such changes for many
453 species would be very challenging. However, in the specific landscapes studied here we have
454 no evidence of gross changes in the composition of native vegetation – we found no
455 suggestion that moist tropical forests in Ghana were once more open (Phalan 2009), while in
456 northern India we identified only two grassland-dependent bird species (out of 174 species
457 studied; Phalan et al., 2011). We therefore suggest that our baselines provide a reasonable
458 characterization of species' population sizes in each region prior to the advent of farming.
459
460
461 Turning to other concerns about land sparing, there is a perception that land sharing is more
462 compatible with smallholder farming (e.g. Fischer et al., 2017). However, land sparing could
463 also be implemented in ways which support and are supported by smallholders (Chandler et
464 al. 2013). There are concerns that the range and magnitude of ecosystem services could
465 decrease with a shift from land sharing to sparing (Fischer et al., 2017). However, land
466 sparing does not mean prioritising high yields at any cost, and will only be viable if it sustains
467 productive landscapes, including the ecosystem services they provide. We lack data to
468 predict the long-term implications of contrasting approaches to land use for soils (Dupouey et
469 al., 2002) and ecosystem services (Kremen and Miles 2012), but there is growing evidence
470 that land sparing would be preferable for carbon storage and sequestration (Gilroy et al.,

2014b; Lamb et al., 2016b; Williams et al., forthcoming). However more evidence is needed before general conclusions can be drawn.

One last caveat is that our calculations assume that the low-yielding areas assessed during field surveys are representative of the agriculture that would be supported under land sharing. However, this assumption may be false – it is likely that farmers who currently farm at low yields include those who care most about nature, and/or who farm in more remote areas close to native vegetation patches which boost on-farm biodiversity via spill-over (as in Gilroy et al., 2014a). If agri-environment schemes were rolled out more broadly, these would support less biodiversity if newly-enrolled farmers cared less about nature or newly-enrolled farms were more distant from native vegetation. This would reduce estimated population sizes and population viabilities under land sharing below those suggested here.

Most current policy interventions for reconciling biodiversity conservation with agricultural production are conceptually aligned with land sharing (e.g. calls by the Ghanaian Ministry of Food and Agriculture [2002] for greater use of agro-forestry and mixed farming; government encouragement of agro-forestry in India [Ravindranath et al., 2008]; and Pillar Two funding under the Common Agricultural Policy [IoG, 2018]). Protected area establishment and sustainable intensification initiatives are also widespread, but land-sparing policies to link and coordinate such initiatives are rare (Phalan et al. 2016). If land sharing interventions were proving sufficient to slow biodiversity loss, there might be little incentive to consider land sparing. Extinctions and population declines, however, continue. Recently, this dire situation has prompted calls for greatly increased allocation of land for conserving wild nature: the Half-Earth concept (Wilson 2016) and Nature Needs Half (Nature Needs Half, 2017). To scale-up conservation to such an extent without compromising agricultural production would

require sustainable high-yield farming in areas that remain cultivated (Balmford and Green 2017).

We conclude by reiterating that imperfections in the implementation of land sparing substantially reduce estimated population viabilities and hence the benefits of such an approach. However, even if such imperfections are not addressed they are unlikely to be of sufficient magnitude as to make land sharing a more desirable option. For wild species – especially those with small global ranges – land sparing remains the least bad approach for reconciling conservation and food production. The challenge remains to develop and test policy mechanisms that link yield growth directly to reductions in farmland area (or constraints on its expansion), and to ensure spared native vegetation is of high quality.

Authors' contributions

BB, REG and AB conceived the idea, and designed the methods; BP and MO acquired the data], which BB analysed; BB and AB drafted the paper and REG and BP critically revised it. All authors approved the final version for publication.

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520 **Data accessibility**

521 All data used in the article was sourced from the published literature and citations to all
522 sources are provided in the text.

523

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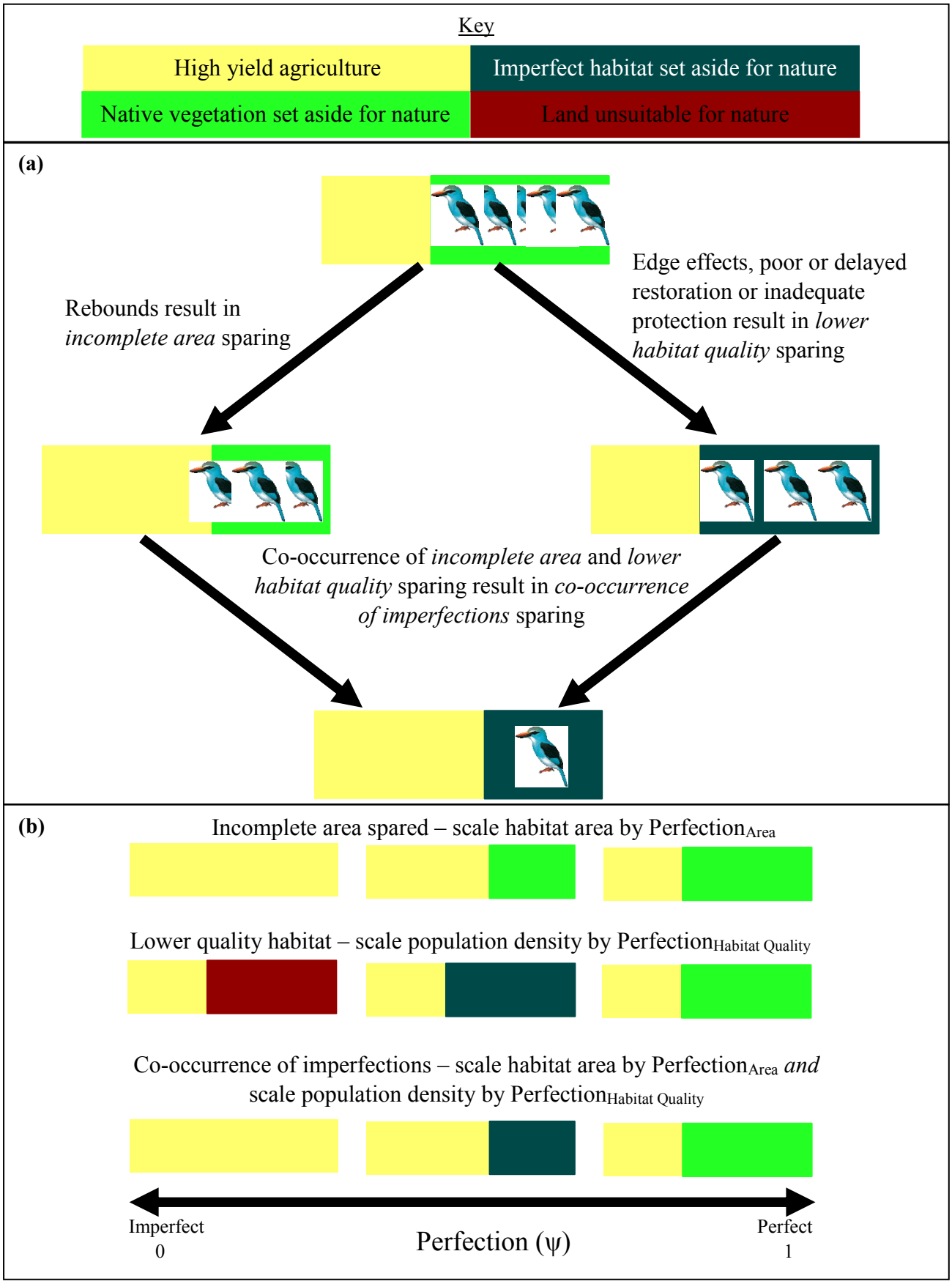
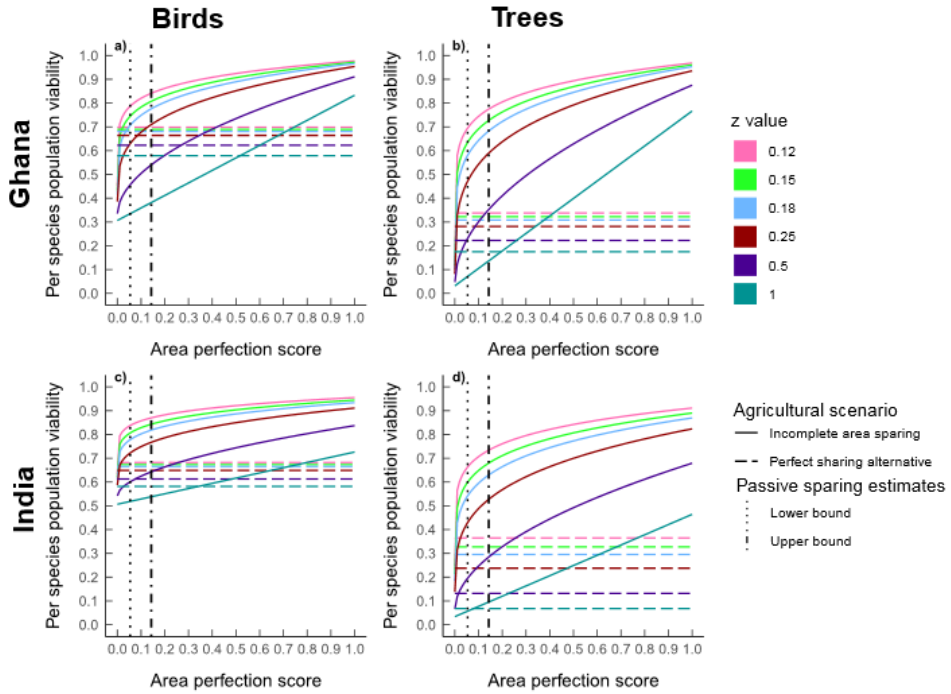

Key
High yield agriculture
Imperfect habitat set aside for nature
Native vegetation set aside for nature
Land unsuitable for nature
(a)
Rebounds result in *incomplete area* sparing
Edge effects, poor or delayed restoration or inadequate protection result in *lower habitat quality* sparing
Co-occurrence of *incomplete area* and *lower habitat quality* sparing result in *co-occurrence of imperfections* sparing
(b)
Incomplete area spared – scale habitat area by Perfection$_{Area}$
Lower quality habitat – scale population density by Perfection$_{Habitat\ Quality}$
Co-occurrence of imperfections – scale habitat area by Perfection$_{Area}$ *and* scale population density by Perfection$_{Habitat\ Quality}$
Imperfect
0
Perfection (ψ)
Perfect
1

Figure 1 – Potential imperfections in the implementation of land sparing.

Cartoons illustrate (a) how land sparing may be imperfect; and (b) the gradients in imperfection which we modelled. Bars represent regions composed of native vegetation (green) and high yield farmland (yellow). Previous analyses, [top of (a)] assume that yield increases result in proportionate decreases in the area under farming and corresponding increases in the area of native vegetation, which is the same quality for wild species as that assessed during surveys. Under incomplete area sparing [middle left of (a)] a portion of the land that could, in principle, be spared is used for additional high-yield farming. Under lower habitat quality sparing [middle right of (a)], spared land is of lower quality. These imperfections can co-occur [bottom of (a)]. We model these imperfections along a gradient [shown in (b)] from perfect land sparing [extreme right of (b)] to wholly imperfect sparing. For incomplete area sparing [top of (b)] the area spared land is reduced so that when wholly imperfect no native vegetation is spared [top left of (b)]. For lower habitat quality sparing [middle of (b)] the population density of a species in native vegetation is reduced until eventually the native vegetation supports none of it [middle left of (b)]. For co-occurrence of imperfection sparing [bottom of (b)], the area of spared land and the population density of a species in native vegetation are reduced. ψ=perfection score.


Birds
Trees
Ghana
India
a)
b)
c)
d)
Per species population viability
Area perfection score
z value
0.12
0.15
0.18
0.25
0.5
1
Agricultural scenario
Incomplete area sparing
Perfect sharing alternative
Passive sparing estimates
Lower bound
Upper bound

794 Figure 2 – Population viabilities under incomplete area sparing, for the 2007 production
795 target.
796 Mean population viability in relation to the perfection of land sparing (solid lines), when
797 rebound effect cause incomplete area sparing. Different *z*-values (colours) reflect uncertainty
798 in the relationship between population size and viability. Curved lines show mean population
799 viability under land sparing, with dashed horizontal lines showing mean viability (for
800 corresponding *z*-values) under perfect sharing. Lines for imperfect land sparing and perfect
801 land sharing lines cross at the point of indifference between the two alternatives. To the right
802 of these points, imperfect land sparing outperforms sharing. Vertical lines represent upper-
803 and lower-bound empirical estimates of passive sparing (as observed in Ewers et al. 2009).
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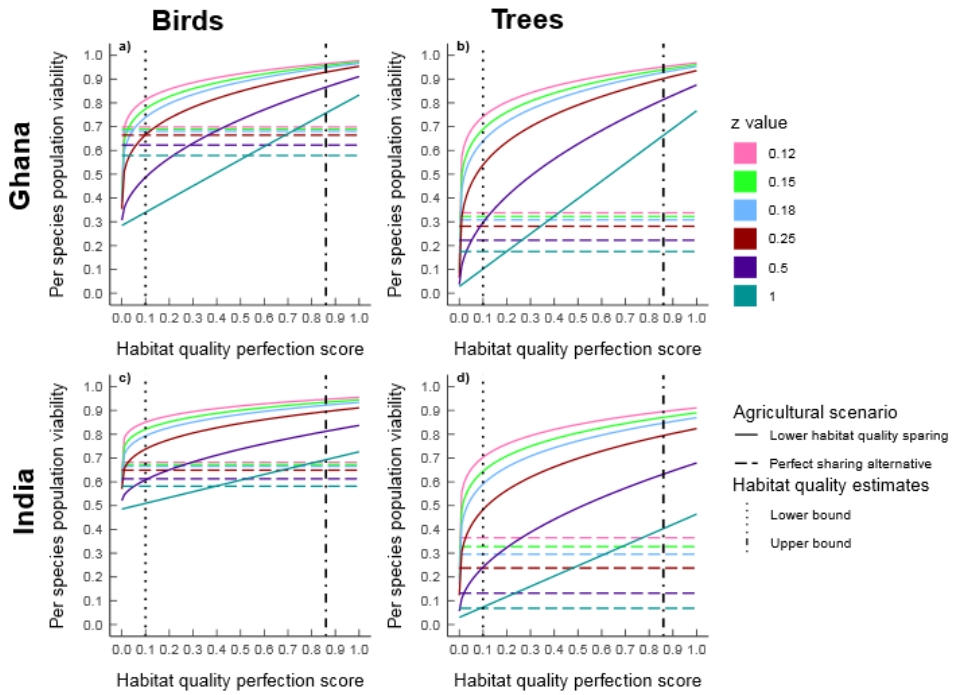
Birds
Trees
Ghana
India
a)
b)
c)
d)
Per species population viability
Habitat quality perfection score
z value
0.12
0.15
0.18
0.25
0.5
1
Agricultural scenario
Lower habitat quality sparing
Perfect sharing alternative
Habitat quality estimates
Lower bound
Upper bound

816 Figure 3 – Population viabilities under lower habitat quality sparing, for the 2007 production
817 target.
818 Mean population viability in relation to the perfection of land sparing (solid lines), when poor
819 or delayed restoration, inadequate protection, or edge effects results in lower habitat quality
820 sparing. As in Fig. 2 different *z*-values (colours) reflect uncertainty in the relationship
821 between population size and viability, curved lines show mean population viability under
822 land sparing, dashed horizontal lines show mean viability (for corresponding *z*-values) under
823 perfect sharing, and vertical lines represent upper- and lower-bound estimates for likely
824 habitat perfections (see text). To the right of the points where corresponding lines for
825 imperfect land sparing and perfect land sharing cross, imperfect land sparing outperforms
826 sharing.
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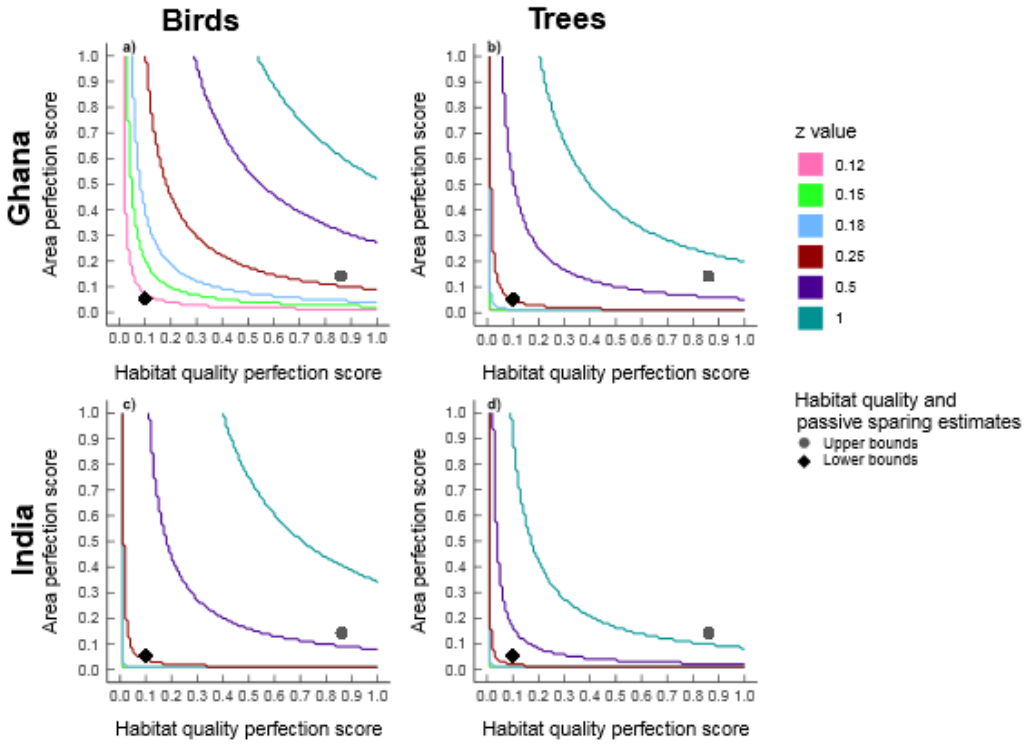
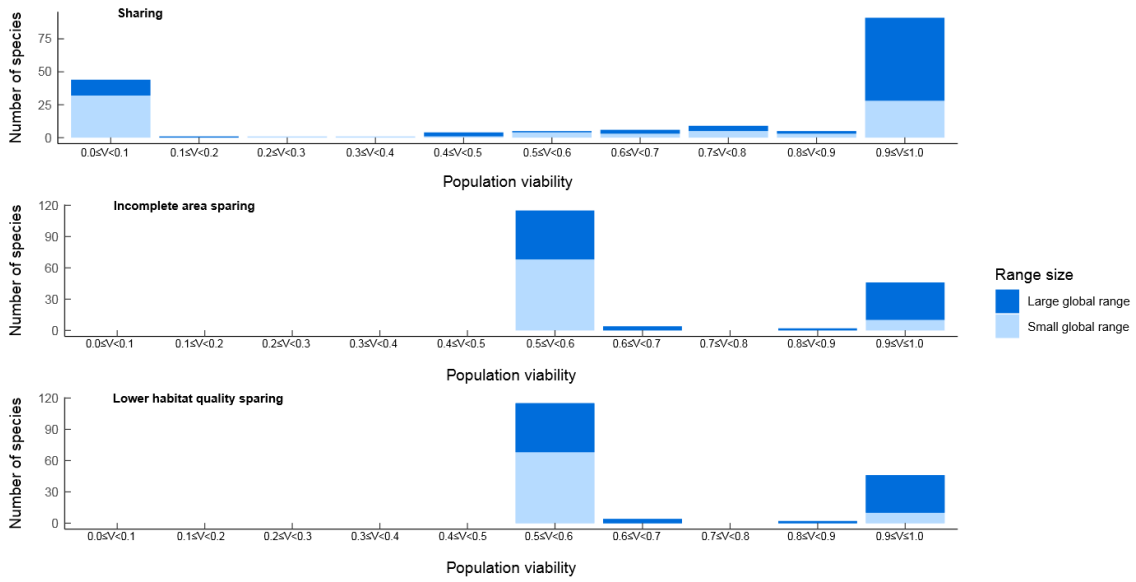

Birds
Trees
Ghana
India
a)
b)
c)
d)
Area perfection score
Habitat quality perfection score
z value
0.12
0.15
0.18
0.25
0.5
1
Habitat quality and
passive sparing estimates
Upper bounds
Lower bounds

836

837

838

839 Figure 4 – Combinations of perfection scores resulting in indifference between land sparing
840 and sharing given co-occurrence of imperfections in land sparing, for the 2007 production
841 target.
842 As in Figs. 2 and 3, different *z*-values (colours) reflect uncertainty in the relationship between
843 population size and viability. Above lines, land sparing outperforms land sharing. The points
844 on each plot represent combinations of our benchmark perfection scores (upper bound-upper
845 bound [grey circle]; and lower bound-lower bound [black diamond]), and reveal that in most
846 cases even co-occurring incomplete area and lower habitat quality sparing outperforms land
847 sharing, given plausible values of *z* (0.12-0.5).
848


Sharing
Number of species
75
50
25
0
0.0≤V<0.1
0.1≤V<0.2
0.2≤V<0.3
0.3≤V<0.4
0.4≤V<0.5
0.5≤V<0.6
0.6≤V<0.7
0.7≤V<0.8
0.8≤V<0.9
0.9≤V≤1.0
Population viability
Incomplete area sparing
Number of species
120
90
60
30
0
Population viability
Lower habitat quality sparing
Number of species
120
90
60
30
0
Population viability
Range size
Large global range
Small global range

849

850

851

852 Figure 5 – frequency distributions of population viabilities of individual species at the point
853 of indifference between land sharing, incomplete area sparing and lower habitat quality
854 sparing.
855 Data are for Ghanaian birds, for the 2007 production target, and for z=0.25 (see also Table
856 S1; Fig. S4). Species are divided into those with large and small global ranges (as reported in
857 Phalan et al., 2011). Individual species viabilities (V) are calculated at the point of
858 indifference – in terms of means species population viabilities – between land sparing and
859 sharing, but when disaggregated to species level both forms of imperfect sparing result in
860 higher population viabilities (compared to those under land sharing) for species with small
861 global ranges, and lower ones for large-range species.